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Geographic Patterns of Diversity in Benthic Marine Algae[1]

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ABSTRACT: Study of the geography of benthic marine algae has traditionally taken the form of descriptions of floras, analyses of floras in terms of floristic components, comparison of the flora and vegetation of one area with that of another area, and delineation of floristic provinces. The concept of genetic diversity transcends floristic analysis and leads to the recognition of geographic diversity patterns related to, but not coincidental with, floristic patterns. Unlike vascular plants, in which the ratio of tropical to nontropical species is 2 : 1, benthic marine algae reach their peak of species diversity on transitional warm-cool temperate coasts. Lowest species diversity, as would be expected, is exhibited by the arctic and antarctic floras. The Mediterranean flora is highly diverse. In the Atlantic, the cold-water flora is richest in the east, while the warm-water flora is richest in the west. In the vastly broader Pacific, the cold-water flora is equally rich on both sides, but again the warm-water flora is richest in the west. Moreover, many warm-water species extend into the Indian Ocean. The Pacific is complicated by the presence of a myriad of islands of various sizes, shapes, structure, ages, and degree of isolation. In the Indian Ocean, the high species diversity of the floras of Natal and southwestern Australia is matched by that of India, while intervening equatorial areas are significantly less rich. Taxonomic diversity is an assessment of the evenness of distribution of the species of a local flora compared to the regional taxonomic spectrum. The highest degree of intrageneric morphological diversity is exhibited by *Codium* and *Caulerpa*.

THE GEOGRAPHY OF benthic marine algae, or seaweeds as they are commonly called, has traditionally encompassed five aspects: first, description of the flora of a particular area varying in size from a single site to an oceanic region; second, analysis of this flora in terms of floristic components, such as cosmopolitan species, pantropical species, boreal species, endemic species, and introduced species; third, an attempt to explain the relative importance of these different components by considering such factors as migration pathways, currents, salinity patterns, and temperature patterns; fourth, comparison of this flora with those of other areas, sometimes entailing comparisons of hydrographic factors and habitat diversity; and fifth, delineation of large-scale floristic patterns, usually termed regions or provinces, based on a consideration of various local floras.

All biogeographic studies result in information on diversity, but most marine floristic workers do nothing more with the concept than determine the total number of species, usually broken down to classes (blue-greens, reds, browns, yellow-greens, greens). Sometimes they consider the significance of the relative size of these components, such as the ratio of the number of species of red algae to the number of species of brown algae, a ratio used to indicate degree of tropicality.

When I looked to see what had been published on diversity in seaweeds, I found only one author who had addressed the topic directly, although briefly, and that was Klaus Lüning in his remarkably informative book,

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Meeresbotanik (1985), with a revised edition in English called *Seaweeds* (1990). As used by Lüning, the term *diversity* refers only to number of species. The literature on diversity of animals and terrestrial plants does not present such a simple picture. My master's thesis dealt with the geographic distribution of the seaweeds of California, and in the subsequent period of more than 40 years, encompassing several studies of insular floras, I have given much thought to the concept of diversity. Were it not for this previous experience, I would have been hopelessly confused by the literature. Quoting from Goldsmith and Harrison (1976:109): "Diversity is a concept that has been interpreted in different ways by different workers depending principally on their scale of study.... In spite of the confusion about the meaning of diversity, it is an important concept, principally because several workers have suggested that high diversity is related to stability."

In my opinion, whether or not a relationship exists between high diversity and stability has little to do with the importance of the concept of diversity, which in any case is useful when playing geographic games and as an indicator of the deterioration or amelioration of the environment.

The confusion in the literature obviously results from differences in background, information, interest, and point of view of the various authors. As a common noun, diversity need not be defined, but for biological purposes it assumes special meanings with each change in adjective. For example, we encounter marine, terrestrial, and freshwater diversity with reference to habitat, and arctic, temperate, and tropical diversity with reference to latitude. Both sets of terms refer to *species diversity*, which biogeographers define simply as the total number of species present in a given area. Ecologists, on the other hand, usually consider the number of species to be only one element of species diversity, which they call *richness*, the second element being *equitability* or *evenness* in the representation of individuals of the component species. Like all other biogeographers, I shall ignore evenness when speaking of species diversity. *Pattern diversity*, related to stratification, zonation, periodicity, patchiness, food webs, and microhabitats, is a term employed by Odum (1983:409, 418). This ecological concept, in my opinion, is not coordinate with species diversity, but rather is an important factor accounting for species diversity in accordance with Whittaker's conclusion that diversity begets diversity (Whittaker 1975:103). Another related concept recognized by Odum (1983:409, 425) is *genetic diversity*, which, like pattern diversity, I consider an important factor accounting for species diversity rather than being a discrete coordinate concept.

Literature on the concept of species diversity deals almost exclusively with the search for the causes of perceived diversity gradients or differences. Here is where confusion reigns, because for almost every hypothesis, conflicting data can be found. Whittaker (1975:102) shed light on the problem by pointing out what should have been made obvious by other biological disciplines, namely, that each factor affecting species diversity affects individual taxonomic groups uniquely, and although it is true that these factors operate in a generally similar fashion for many large groups of organisms, resulting in generally perceived diversity gradients, some groups constitute notable exceptions. Whittaker concluded that in some special cases, we can make reasonable predictions about diversity. For example, the number of species of birds can be predicted by considering the complexity of vegetation structure. A vegetative pattern that includes a high canopy of trees along with open shrubby areas will support a highly diverse bird fauna compared to uniformly open areas. In other cases, species diversity must be regarded as a product of evolution that is interesting to observe and capable of being interpreted, but not predictable.

I was greatly relieved to read this admission after having encountered repeatedly the generalization that the number of species increases markedly from the poles to the equator, knowing from experience that benthic marine algae do not fit this mold. Instead, they fall into Whittaker's "other cases" in which we must emphasize evolution, or the accumulation of new species and the extinction of old

species, in addition to ongoing ecological factors.

Seaweeds constitute a relatively small taxonomic group, probably not many more than 6500 or 7000 species. (Estimates of number of species, unless a reference is cited, are original or based on figures compiled by Lüning [1990].) Localities notably poor in species are found at very high latitudes. For example, only two conspicuous species survive at McMurdo Station in Antarctica (77° 30′ S), but the number increases to about a dozen at the northern end of McMurdo Sound (Richard Moe, pers. comm.). A decrease in latitude is accompanied by a marked increase in the number of species, reaching about 110 on the Antarctic Peninsula at 62° to 68° S (Moe and DeLaca 1976). In the arctic, the northernmost collections are from near the northern tip of Greenland (82° N) and comprise 21 species (Lund 1951). At somewhat lower latitudes, the Canadian arctic as a whole supports about 170 species (Lee 1980).

In contrast, greatest diversity is exhibited by the floras of transitional warm-cool temperate coasts, particularly those of southern Australia (about 1100 species), the Pacific coast of North America (at least 1000 species), central Japan (800 to 900 species), and South Africa (about 600 species). Another markedly diverse temperate flora is that of the Mediterranean Sea, a basin rather than an oceanic region, whose richness (about 1000 species) can be explained by its geological history, involving compartmentation into relatively isolated parts, each of which harbors endemic species. The complex region extending from the Malay Peninsula to the Philippines, sometimes called the Asiatic Mediterranean, with its thousands of islands and numerous relatively isolated basins, is poorly known phycologically, but will undoubtedly prove to be the richest tropical area (800 to 1000 species).

Each of the major oceans exhibits geographical patterns of species diversity. In the Atlantic, the cold-water flora (about 750 species) is richest in the east, from Portugal through Norway, while the warm-water flora (also about 750 species) is richest in the west, covering a very large area that straddles the equator from Brazil to Bermuda. The Canary Islands, despite their position in the eastern Atlantic, have a rich flora as a result of the concurrence of floristic elements from the tropical western Atlantic, the North Atlantic, and the Mediterranean.

In the vastly broader Pacific, the cold-water flora is equally rich on both sides, but again the warm-water flora is richest in the west, extending from New South Wales to central Japan. The impoverished flora of the eastern Pacific has not yet been satisfactorily explained, but it may be related to the cyclical shift in latitude of the major oceanic current system, a phenomenon called El Niño, which results in a particular area being subjected to unusually high or low temperatures periodically. The poverty of the flora may also be related to the lack of diversity of habitat, because the entire Pacific coast is emerging and is mostly exposed to heavy wave action. It is disappointing to find so few species of common tropical genera, especially siphonous green algae (*Caulerpa*, *Halimeda*, the Udoteaceae). The contrast between tropical Pacific Mexico and Atlantic Mexico is sharp. There is no place in Pacific Mexico comparable to Yucatán, where one can snorkel along sandy shelves and encounter dozens of siphonous green algae.

The Pacific Ocean, especially the western and central areas, is complicated by the presence of a myriad of islands of various forms, structure, ages, stability, and degree of isolation. Considerations of insular colonization and endemism apply here to various individual islands and groups of islands with strikingly different results. In general, large volcanic islands can be expected to support more species than small volcanic islands or coral atolls. Approximately 300 species have been recorded from the Hawaiian Islands. In contrast to the very high rate of endemism of Hawaiian flowering plants, which is attributed to the isolation of this archipelago, endemism among Hawaiian seaweeds is relatively low. Great distance from other land masses and hence other floras, however, is not essential for the evolution of endemic species. The Channel Islands of southern California, which are coastal, and those oceanic islands of Mexico that are within 400 km of the

mainland, namely Isla Guadalupe and Rocas Alijos, have a small number of endemic species that may be cast ashore on the mainland, but are never found growing there.

The situation in the Indian Ocean is complex, the high diversity of the floras of Natal and southwestern Australia being matched by that of India, while intervening equatorial areas are significantly less rich, even though they share species with the equatorial Pacific.

These geographic patterns of species diversity result from the interplay of historical and ongoing factors. Among historical factors, changes in sea level as related to the accumulation of polar ice caps and upward or downward tectonic displacement of land masses have affected the existence of suitable habitats. The formation and horizontal movement of discrete continents and their partial fragmentation have affected the distribution of ancestral forms by providing bridges at one time, barriers at another time. Moreover, changes in the distribution of land masses have resulted in changes in the pattern of oceanic currents, which in turn is a major factor in determining the distribution of seaweeds. Paleoecological conditions such as temperature and salinity have affected the rate and effectiveness of selection of mutant forms and their extinction. The rate and direction of evolution within a particular taxonomic group, however, is independent of environmental factors, both historical and ongoing, to varying degrees.

Thus we see that the size of the potential species pool of a region depends on the ancestral forms that reached its shores during the positioning of present-day continents, by the rate and direction of evolution of these ancestral forms, and by the rates and effectiveness of selection and extinction. For specific sites within a region, the potential species pool is greatly modified by ongoing environmental factors, such as habitat diversity and temperature distribution, especially as related to currents, as well as by the effectiveness of dispersal and establishment of the potentially available species. Although about 350 species are known from any given region of California, an unusually rich site supports no more than 150 species while stressed sites have as few as 20 species.

An interesting example of a specific flora within a potential species pool is provided by the Farallon Islands, very close to San Francisco. These rocky maritime habitats have been alternately emergent and submergent during Pleistocene glaciation. As the sea level was lowered, exposing the shores of the islands, opportunities arose for propagules from intertidal mainland communities to establish themselves in pristine territory. Factors of chance and competition obviously operated in this case since it turns out that several common mainland species are absent on the islands. The shallow and moderately deep subtidal flora, on the other hand, is like that of the adjacent mainland, while the deep-water flora is part of a community that extends from Canada to Mexico.

Even more interesting is Cordell Bank, a seamount that is part of the same piece of land as the Farallon Islands. The shallowest depth is 35 m. After identifying the seaweeds collected by divers, my assistant (Dr. Kathy Ann Miller) incubated a piece of organic substrate and obtained a juvenile kelp, much to our surprise since the divers found no kelps. The juvenile was grown in the laboratory of Dr. Phillip A. Lebednik at Diablo Canyon, California, and turned out to be *Nereocystis luetkeana*, the bull kelp, whose sporophyte is not known to grow at depths below 22 m and usually grows at much shallower depths. It is fascinating to contemplate the microscopic filamentous gametophyte surviving vegetatively for centuries, waiting for sea level to become low enough to allow sufficient light for the sporophyte to develop and thus complete the life history of this species.

Although it is not possible here to discuss possible explanations for each geographic pattern of species diversity mentioned earlier, I will consider two of them briefly.

At one end of the spectrum, the very low diversity of McMurdo Sound can be explained almost solely by the present-day environment, which is extremely hostile, both because of ice-scouring and because of the extremely low quantities of heat and light that are available at such a high latitude.

At the other end of the spectrum, an explanation of the richness of transitional warm-cool temperate shores requires consideration

of both historical and ongoing factors. All of these rich shores were blessed with many ancestral forms that have speciated markedly. I suggest three environmental factors that may have enhanced selection and retention of new species: temperature, photoperiod, and tide-induced desiccation. We know from culture experiments that temperature and photoperiod are critical factors in survival and reproduction. Desiccation, although not always critical, certainly is important. Since most of these coastlines have a N/S orientation, there are corresponding linear temperature and photoperiod gradients. Each species at present has definite latitudinal limits, a phenomenon obviously not applicable to the tropics. In addition, these shores often have tides of great amplitude, and it seems reasonable to assume that tide-induced desiccation, whether favorable or unfavorable to the alga, is favorable to evolutionary selection. I should also mention Whittaker's aphorism, "diversity begets diversity." As new species of animals are accumulated, new niches for plants are provided and new selection pressures come into play, such as herbivory, which selects for those seaweeds that taste the worst.

Finally, I want to suggest two kinds of diversity that I have found conceptually useful but have never encountered in the literature. One, which may be called *taxonomic diversity*, is an assessment of the evenness of distribution of the species of a local flora compared to the regional taxonomic spectrum. For example, several years ago when I was studying the flora of central San Francisco Bay, I found that surprisingly many outer-coast species are able to survive in this environment of erratic salinity changes. Those that are excluded because of the lack of highly exposed sites are balanced by protected-water forms, some of which are cosmopolitan harbor dwellers. The total number of species, 170, compares favorably with outer-coast areas of equal habitat diversity. I wondered whether this flora is taxonomically diverse. A meaningful and simple way to answer this question is to turn the pages of a regional manual (in this case Abbott and Hollenberg's *Marine algae of California* [1986]), noting how well or how poorly the various parts of the taxonomic spectrum are represented. Because the San Francisco Bay flora includes at least one representative of almost every major order and family, I concluded that it is taxonomically diverse.

The second kind of diversity that I want to introduce is best illustrated by two genera of green algae, *Codium* and *Caulerpa*, both of which are well represented on warm-cool transitional coasts. Both genera are excellent examples of evolutionary variations on a theme. Each genus has a unique structural plan based on coenocytic filaments rather than cells. In *Codium* the filaments intertwine to produce a thallus with gross morphological characters that have only secondary diagnostic value in separating the approximately 100 species. The filaments form a surface layer of photosynthetic branches (utricles) in accordance with various ontogenetic patterns, apparently reflecting ancient phylogenetic events. Figure 1, in which the utricles from several species have been drawn to the same scale, shows the great anatomical diversity expressed within the confines of a basic plan. At the macrosopic level, the thalli exhibit a broad range of habit, partly displayed in Figure 2. *Codium setchellii* (a) forms a carpet that adheres firmly to the substrate, while *C. bursa* (b) is like a tennis ball. *Codium cuneatum* (c) is erect and dichotomously branched, with the branches cylindrical or somewhat compressed. In *C. platylobium* (d) these dichotomous branches are completely flat and reminiscent of a piece of felt.

In *Caulerpa*, the plant body is a large coenocytic tube that stands by itself, without intertwining, supported by a heavy wall reinforced with cross-struts, called trabeculae. Four of the approximately 75 species are shown in Figure 3. *Caulerpa* is a remarkable mimic, as evidenced by such specific epithets as *cactoides*, *cupressoides*, *ericoides*, *lycopodioides*, and *taxifolia*.

This richness of forms may be called *intrageneric morphological diversity*, which presumably reflects *intrageneric genetic diversity*. Both *Codium* and *Caulerpa* are rich in species. Additionally, both genera are diverse in the popular sense of the word. In contrast are *Ceramium* and *Polysiphonia* in the red algae,

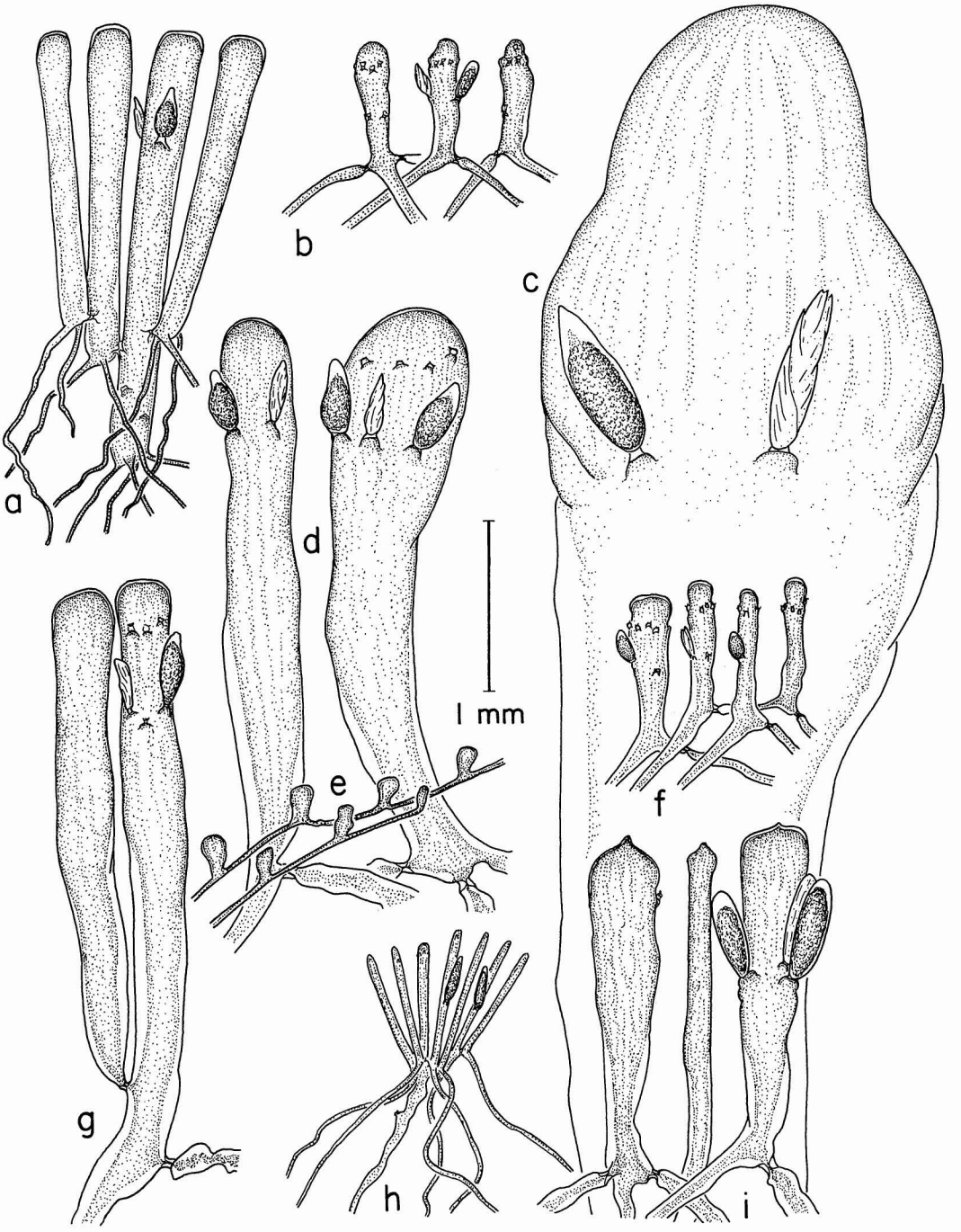

FIGURE 1. Utricles from various species of *Codium* drawn to same scale. *a*, *C. ritteri*; *b*, *C. laminarioides*; *c*, *C. megalophysum*; *d*, *C. cylindricum*; *e*, *C. petaloideum*; *f*, *C. tomentosum*; *g*, *C. bursa*; *h*, *C. adhaerens*; *i*, *C. fragile* subsp. *atlanticum*.

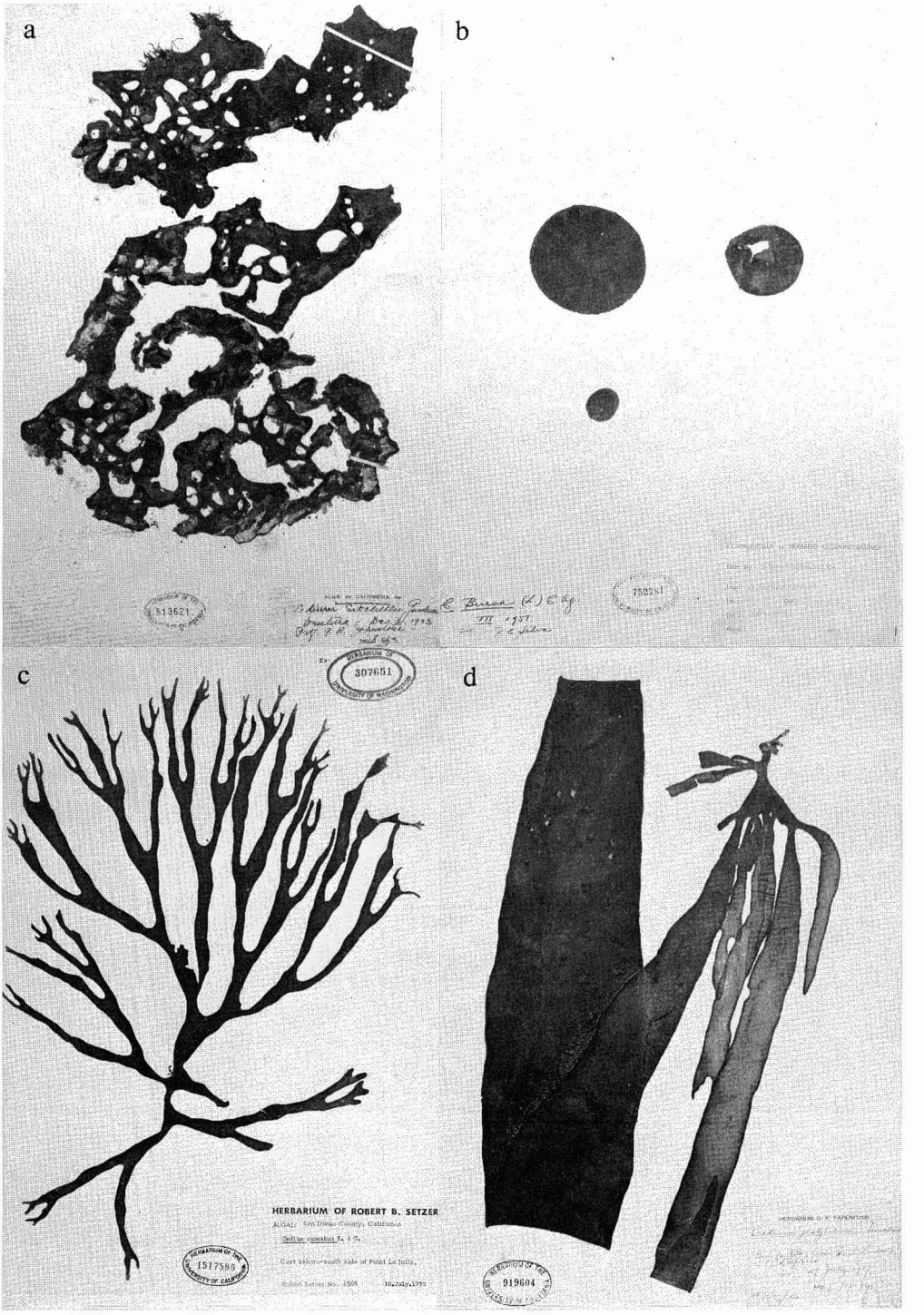

FIGURE 2. Diversity of habit in *Codium*, ca. 1/4. *a*, Adherent crust of *C. setchellii*; *b*, globular thallus of *C. bursa*; *c*, erect, dichotomously branched thallus of *C. cuneatum*, with cylindrical or somewhat compressed branches; *d*, erect, dichotomously branched thallus of *C. platylobium*, with completely flat and feltlike branches.

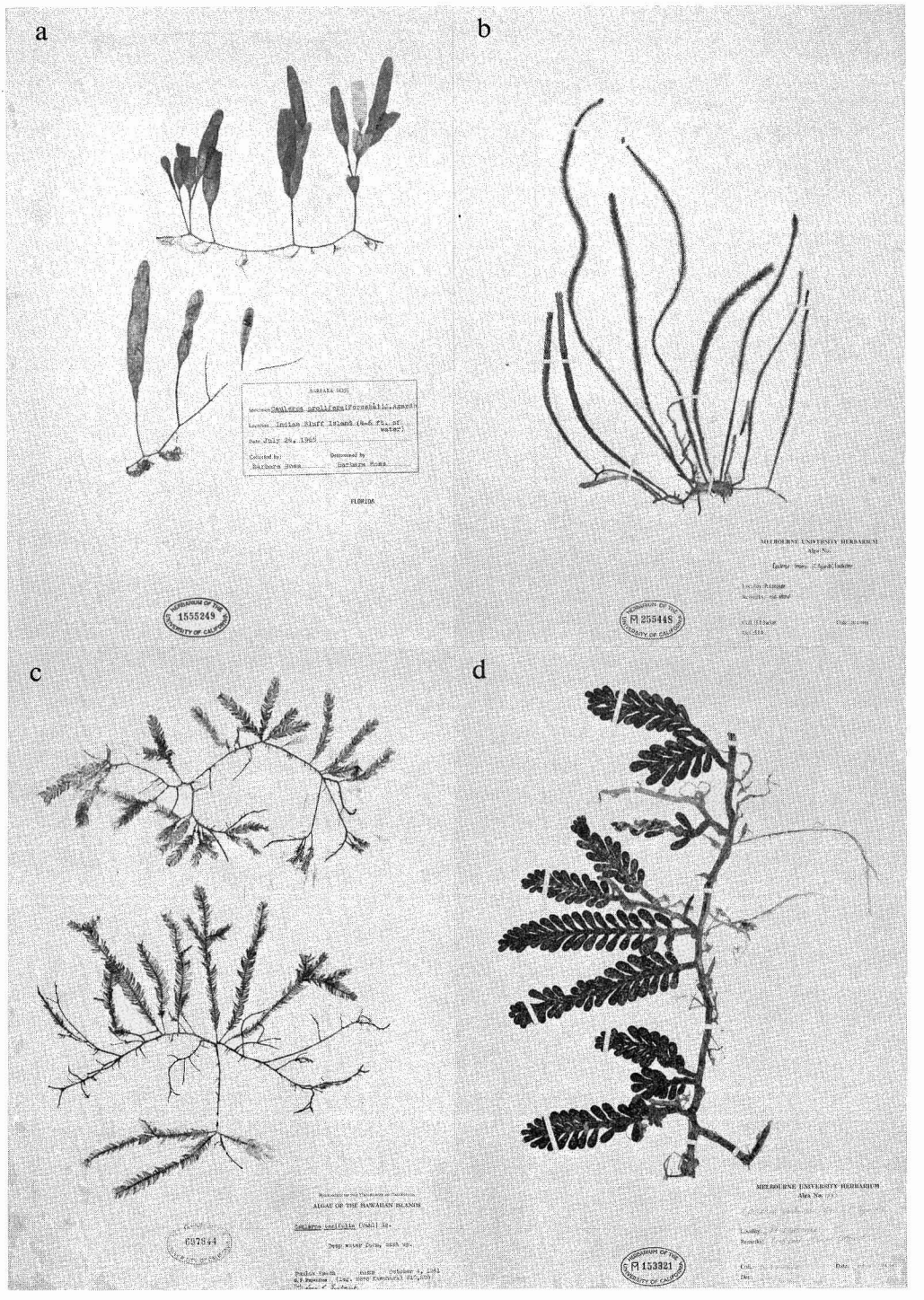

FIGURE 3. Diversity of habit in *Caulerpa*, ca. 1/4. *a*, flattened erect branches of *C. prolifera* with the form of entire leaves; *b*, cylindrical erect branches of *C. brownii* covered with short furry branchlets; *c*, flattened erect branches of *C. taxifolia* with oppositely pinnate branchlets; *d*, cylindrical erect branches of *C. cactoides* with oppositely arranged vesiculate branchlets.

Alaria and *Laminaria* in the brown algae, and *Ulva* and *Bryopsis* in the green algae, all genera with many species but in which the morphological variations on the basic pattern are relatively similar.

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